

DR-1580

ORO-747

EFFECTS OF FALLOUT RADIATION ON CROP PRODUCTION

D. D. Killion and M. J. Constantin

Final Report

on

DCPA Work Order No. DAHC 20-70-C-0312

Work Unit No. 3223F

July 3, 1975

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REPORT DOCUMENTATION PAGE		READ INSTRUCTIONS BEFORE COMPLETING FORM
1 REPORT NUMBER ORO-747	2 GOVT ACCESSION NO	3 RECIPIENT'S CATALOG NUMBER
4 TITLE (and Subtitle)  EFFECTS OF FALLOUT RADIATION ON CROP PRODUCTION		5 TYPE OF REPORT & PERIOD COVERED Final Report
		6 PERFORMING ORG REPORT NUMBER
7 AUTHOR(s)  D. D. Killion and M. J. Constantin		8 CONTRACT OR GRANT NUMBER(s) Work Order No. DAHC 20-70-C-0312
9 PERFORMING ORGANIZATION NAME AND ADDRESS Comparative Animal Research Laboratory 1299 Bethel Valley Road Oak Ridge, Tennessee 37830		10 PROGRAM ELEMENT PROJECT, TASK AREA & WORK UNIT NUMBERS Work Unit No. 3223F
11 CONTROLLING OFFICE NAME AND ADDRESS  Defense Civil Preparedness Agency Washington, D.C. 20301		12 REPORT DATE July 3, 1975
		13 NUMBER OF PAGES 46
14 MONITORING AGENCY NAME & ADDRESS (if different from Controlling Office)		15 SECURITY CLASS (of this report)  Unclassified
		15a DECLASSIFICATION DOWNGRADING SCHEDULE
16 DISTRIBUTION STATEMENT (of this Report) Approved for public release; distribution unlimited.		
17 DISTRIBUTION STATEMENT (of the abstract entered in Block 20, if different from Report)		
18 SUPPLEMENTARY NOTES		
19 KEY WORDS (Continue on reverse side if necessary and identify by block number) Gamma irradiation; beta irradiation; crop production; plant sensitivity to ionizing radiation		
20. ABSTRACT (Continue on reverse side if necessary and identify by block number) Data in this report show the following order of plant sensitivity to irradiation: barley > wheat > soybean > corn > potato > alfalfa > rice. Plants were the most sensitive to irradiation during meiosis. Irradiation at high-exposure rates was more damaging than at low-exposure rates. Beta radiation appears to be equally effective as gamma radiation, providing that attenuation by tissue is accounted for in the beta dosimetry.		

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## SUMMARY

In this paper we review the research from six previous reports and also include results from current studies. Research emphasis was placed on total dose, dose rate, type of radiation ( $^{60}\text{Co}$  gamma and/or  $^{90}\text{Y}$  beta), plant species (Seneca wheat, Himalaya barley, CL-8970-S rice, WF-9 x 38-11 corn, Hill and Kent soybeans, Buffalo alfalfa, and Kennebec potato), developmental stage of life cycle, and postirradiation interval.

The order of sensitivity of plant species to irradiation was barley  $\geq$  wheat > soybean  $\geq$  corn > potato > alfalfa > rice. Although plant sensitivity to irradiation has been shown to be related to interphase chromosome volume, apparently morphological development influences this relationship. In terms of seed or grain yield, plants were most sensitive to irradiation during meiosis. High-radiation dose rates were more damaging to plants than low dose rates. This was most evident in the log phase of vegetative growth. Beta radiation (when corrected for dose attenuation) appears to be equivalent to gamma radiation for specific indices of damage. Also important is the postirradiation interval. Annual plants have to reach maturity for the maximum expression of sublethal damage; in perennials, damage may not manifest itself for years.

## INTRODUCTION

A nuclear war would cause crop and livestock production to suffer from exposure to radioactive fallout. In addition, there would be disruption of cultural, harvesting, and processing procedures, and there would be shortages of fuels, fertilizers, and other materials. From the early literature Bell and Cole (1967) summarized information needed to more properly assess livestock and crop-production vulnerability to radioactive-fallout hazards. Brown and Kruzic (1970) discussed a wide range of variables in "Agricultural Vulnerability in the National Entity Survival Context." Sparrow, Schwemmer, and Bottino (1971) reviewed the biological, radiological, and environmental factors related to plant radiosensitivity as applied to agricultural productivity. Ryan, Garza, and Brown (1974) have developed a damage-assessment model for agricultural crops. The model includes ten crop genera and submodels to accommodate data on crop morphology and radiation dose from which the surviving-yield capability is computed. These references define the problem area: the assessment of damage to agricultural production from a nuclear war.

This report focuses attention on one segment of the overall problem: crop plant vulnerability to radioactive fallout as affected by dose, dose rate, kind of radiation, plant species, developmental stage, and postirradiation interval. Data from six previous annual reports (Siemer and Constantin, 1969; Killion and Constantin, 1969, 1970, 1971a, 1972, 1973), as well as from current studies on potatoes and alfalfa, are used in attempting to correlate radiation-induced damage with the above factors.

## MATERIALS AND METHODS

### Plant Material

'Seneca' winter wheat [*Triticum aestivum* (L.) Thell], 'Himalaya' spring barley [*Hordeum vulgare* (L.) Lam.], 'CL-8970-S' rice [*Oryza sativa* L.], 'WF-9 x 38-11' corn [*Zea mays* L.], 'Hill' and 'Kent' soybean [*Glycine max* (L.) Merrill], 'Buffalo' alfalfa [*Medicago sativa* L.], and 'Kennebec' potato [*Solanum tuberosum* L.] plants were used as the experimental material in these studies.

## Irradiation Facilities, Procedures, and Dosimetry

Gamma irradiations were done at a  $^{60}\text{Co}$  variable-dose-rate facility (Cheka, Robinson, Wade, and Gramly, 1971). This facility was calibrated with a 250-R Victoreen chamber that had been compared to one calibrated at the National Bureau of Standards. Additional measurements were made routinely with LiF 1- by 6-mm-rod thermoluminescent dosimeters. A factor of 0.95 was used to convert roentgens to rads.

Beta irradiations were done with either one single-plane sealed source or two single-plane sealed sources of  $^{90}\text{Sr}$ - $^{90}\text{Y}$ , each 28 x 43 cm (Bell, 1970). Dosimetry was determined with hexa (hydroxyethyl) pararosanine cyanide radiochromic liquid (McLaughlin, Hussman, Eisenlohr, and Chalkley, 1971) and thermoluminescent dosimeters calibrated from a  $^{60}\text{Co}$  gamma facility (Cheka, Robinson, Wade, and Gramly, 1971).

The mean beta dose  $D_m$  to the specific meristem was determined from the equation

$$D_m = D_s e^{-\lambda s} \frac{\int e^{-\lambda x} dx}{\int dx}, \quad (1)$$

derived from Loevinger, Japha, and Brownell (1956), where  $D_s$  is the surface dose,  $\lambda$  ( $0.425 \text{ mm}^{-1}$ ) is the determined absorption coefficient,  $s$  is the thickness of the relatively nonsensitive tissue that covered the specific meristem, and  $x$  is the tissue thickness of the specific meristem.

## Plant-Development Stage

### Germinating Seeds

The effects of beta and gamma irradiation on germinating seeds were evaluated in wheat and barley. Seeds were first submerged in distilled water at  $0^\circ\text{C}$  for 16 hr, then placed in 10- by 10-cm petri dishes (100 seeds per dish) lined with water-moistened blotter paper, and allowed to germinate for various periods prior to irradiation. After irradiation, seedlings were cultured until the first leaf was in a steady-state phase of growth (10 to 12 days), at which time height measurements were recorded. (Details have been previously described by Myhill and Konzak, 1967.) For the beta treatments, seeds were arranged with the embryo toward a single-plane beta source. Thickness of the first-leaf meristem was 0.5 mm, and thickness of the relatively nonsensitive tissue (coleoptile and seed coat) covering the meristem was 0.37 mm. Details have been previously described

(Conger, Killion, and Constantin, 1973). Substitution of these values into equation (1) yields

$$D_m = 0.77 D_g.$$

### Seedlings

For the study of soybean responses to gamma and/or beta irradiation, seedlings were grown in 5-cm peat pots in the greenhouse until the unifoliolate leaves unfolded. Seedlings were then irradiated, transplanted to field plots, and grown to maturity at which time they were scored for height and lateral growth (branches) from the cotyledonary node. An irradiation-free period of 10 min was used to transfer the plants from the beta to gamma source. Beta radiation was administered with two single-plane sources mounted on movable supports. With the aid of a portable support, two rows of plants (5 plants per row) were inserted between two beta sources. (Details have been previously described by Killion and Constantin, 1974.) Mean thickness  $x$  of the shoot apical meristem was determined from the equation (Thomas, 1960)

$$x = 4/3 r \quad (2)$$

where  $r$  (1.1 mm) is the determined radius of the meristem which was assumed to be a sphere or, more correctly, a hemisphere. The thickness of the relatively nonsensitive tissue that covered the apical meristem was 0.1 mm. Substitution of these values into equation (1) yields

$$D_m = 0.70 D_g.$$

### Various Stages Throughout the Life Cycle

For other studies with winter wheat, rice, corn, soybean, alfalfa, and potato, plants were either (1) gamma irradiated as seedlings, transplanted to field plots, and grown to maturity, or (2) planted in large containers of fertilized perlite:peat:sand (1:1:1 volume), gamma irradiated at various stages of their life cycle, and grown to maturity under outdoor conditions. Responses measured were grain, seed, tuber, or herbage yield.



## RESULTS

### Germinating Seeds

Sensitivity of germinating wheat and barley seed to gamma irradiation varied with the stage of germination at the time of irradiation (Fig. 1). Sensitivity of both plant species increased with extended periods of germination, reached a maximum, and then decreased. This response was more pronounced for barley than for wheat. Periods of maximal sensitivity were 16 to 24 hr for barley and 40 to 48 hr for wheat, with a reduction to 28 and 50% of controls, respectively.

Additional experiments determined the effects of beta and gamma irradiation at various doses and dose rates at the time of maximal sensitivity—20 hr for barley and 44 hr for wheat (Fig. 1). Results of these experiments are illustrated with response surfaces in Figs. 2 and 3 for wheat and barley, respectively. Analyses of variance for growth of the first leaf showed that a second-order interaction existed for dose, dose rate, and type of radiation for both wheat and barley ( $P < 0.01$ ). However, these analyses should be restricted to the overall test of significance because of the moderate heterogeneity of variances.

In overall effect on wheat seedlings (Fig. 2), gamma radiation was apparently more damaging than beta radiation. Seedling-height response to gamma irradiation resulted in a curved surface over the entire graph area. Seedling height was reduced to 50% of control at 2.8 krad at 11.6 rads/min. Response was different for beta radiation in that the curved surface evolved into a plane section. Seedling height was reduced to a minimum of 65% of control at  $\geq 1.6$  krad at 11.6 rads/min, and at 2.2 and 2.8 krad at 3.4, 7.1, and 11.6 rads/min.

Radiation was more damaging to barley (Fig. 3) than it was to wheat (Fig. 2). In addition, at 1.3 rads/min the dose curves were inflected at the higher doses (i.e., 1.3 rads/min were more damaging to the seedlings than were 3.7 rads/min). Seedling height was reduced to 28 and 31% of control by 2.8 krad of gamma and beta radiation, respectively, at 12.6 rads/min. At the higher doses and dose rates, the response surface evolved into more of a plane section with beta than it did with gamma irradiation.

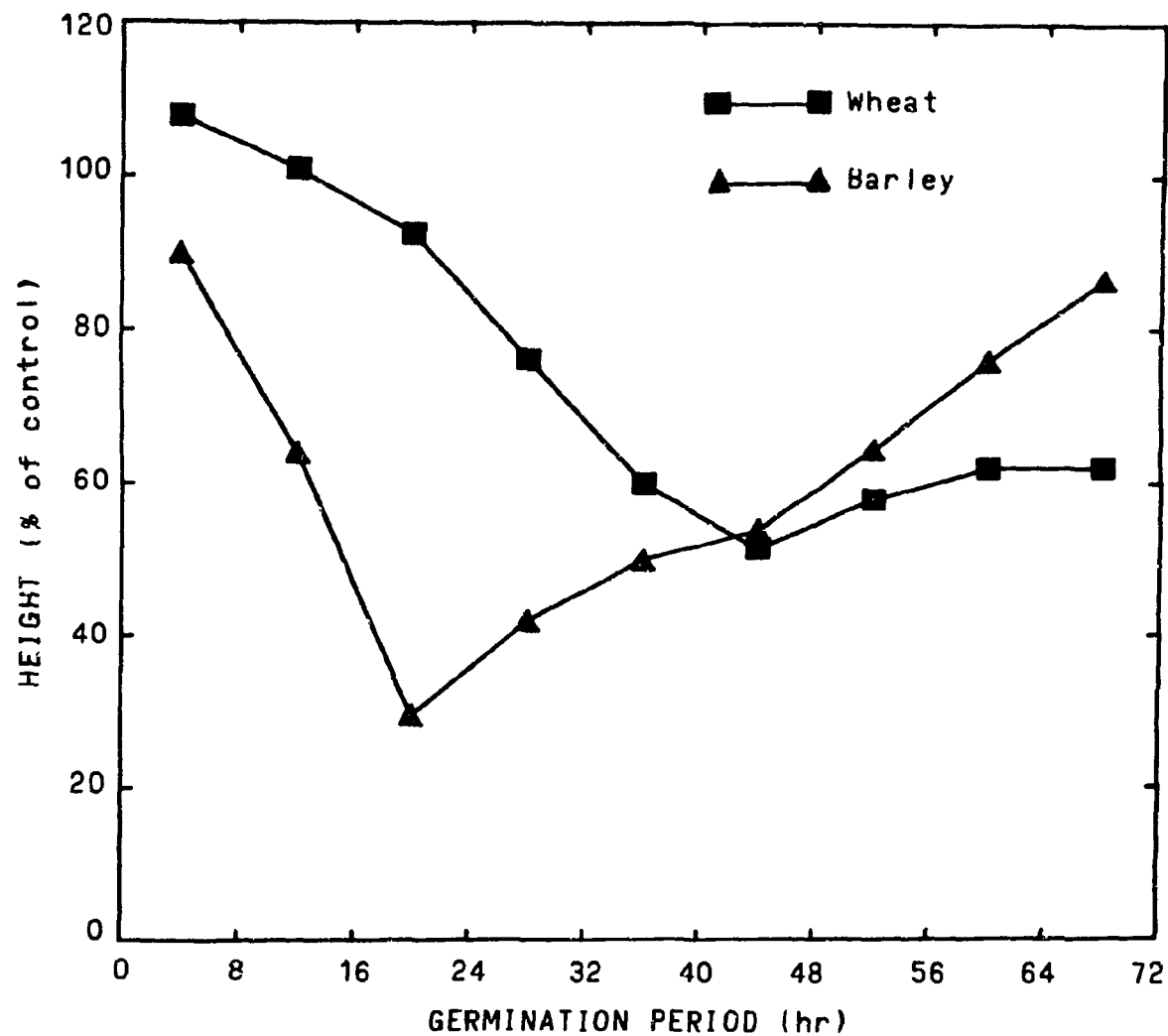


Fig. 1. Effect of 2.4 krad (5 rads/min) of gamma radiation delivered at various periods of germination (8-hr duration) on height of the first leaf of wheat and barley seedlings. Height was recorded in the steady-state phase of first-leaf growth (control; wheat  $16.4 \pm 0.4$  cm; barley  $15.2 \pm 0.5$  cm).

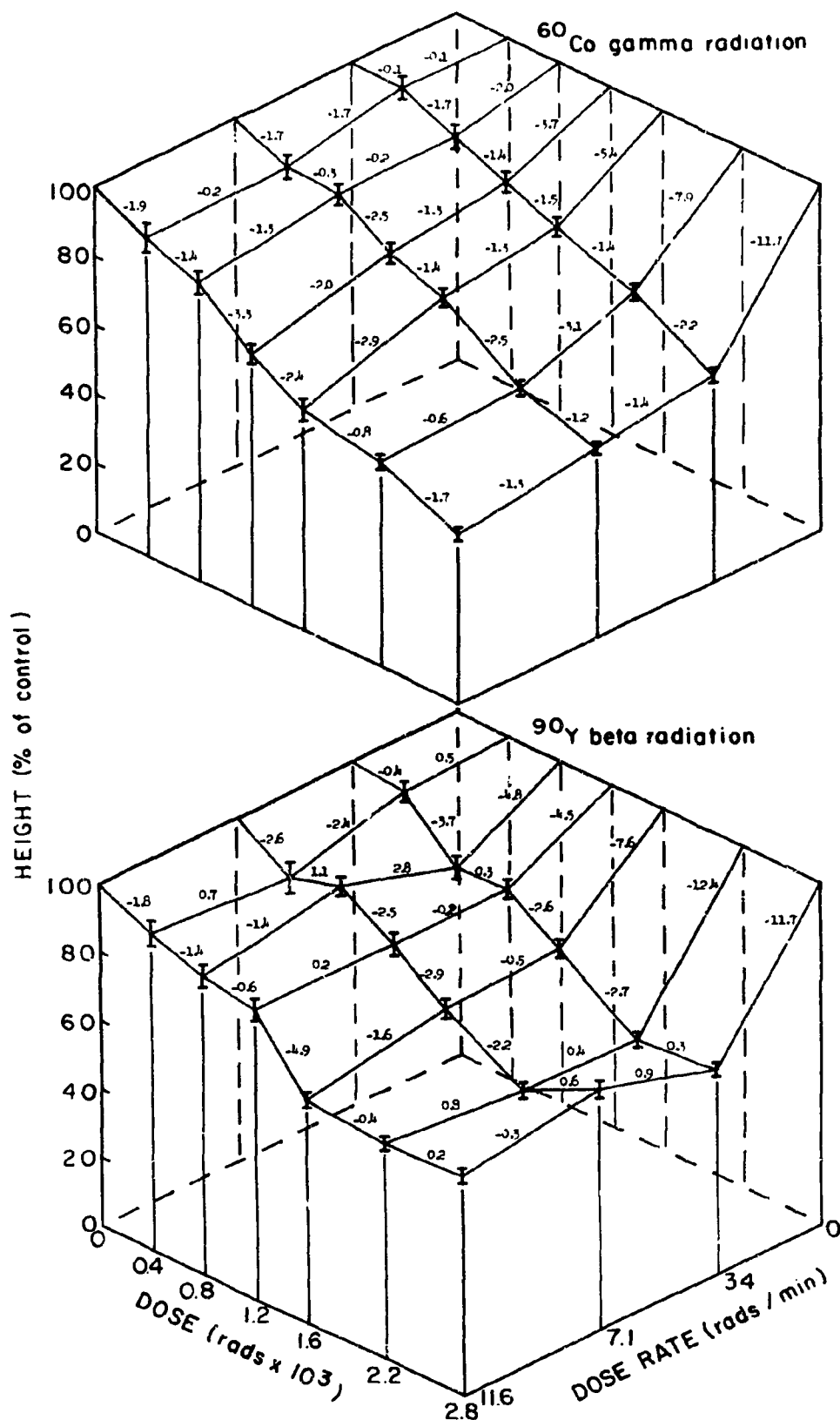


Fig. 2. Effect of gamma or beta radiation at various doses and dose rates on height of the first leaf of wheat seedlings. Seeds were irradiated at 32 hr of germination. Numbers on response surface indicate changes expressed as either  $\% \times 10^{-2}/\text{rad}$  or  $\%-\text{min}/\text{rad}$ . Vertical bars indicate standard errors. Height was recorded in steady-state phase of first-leaf growth (control  $16.4 \pm 0.4$  cm).

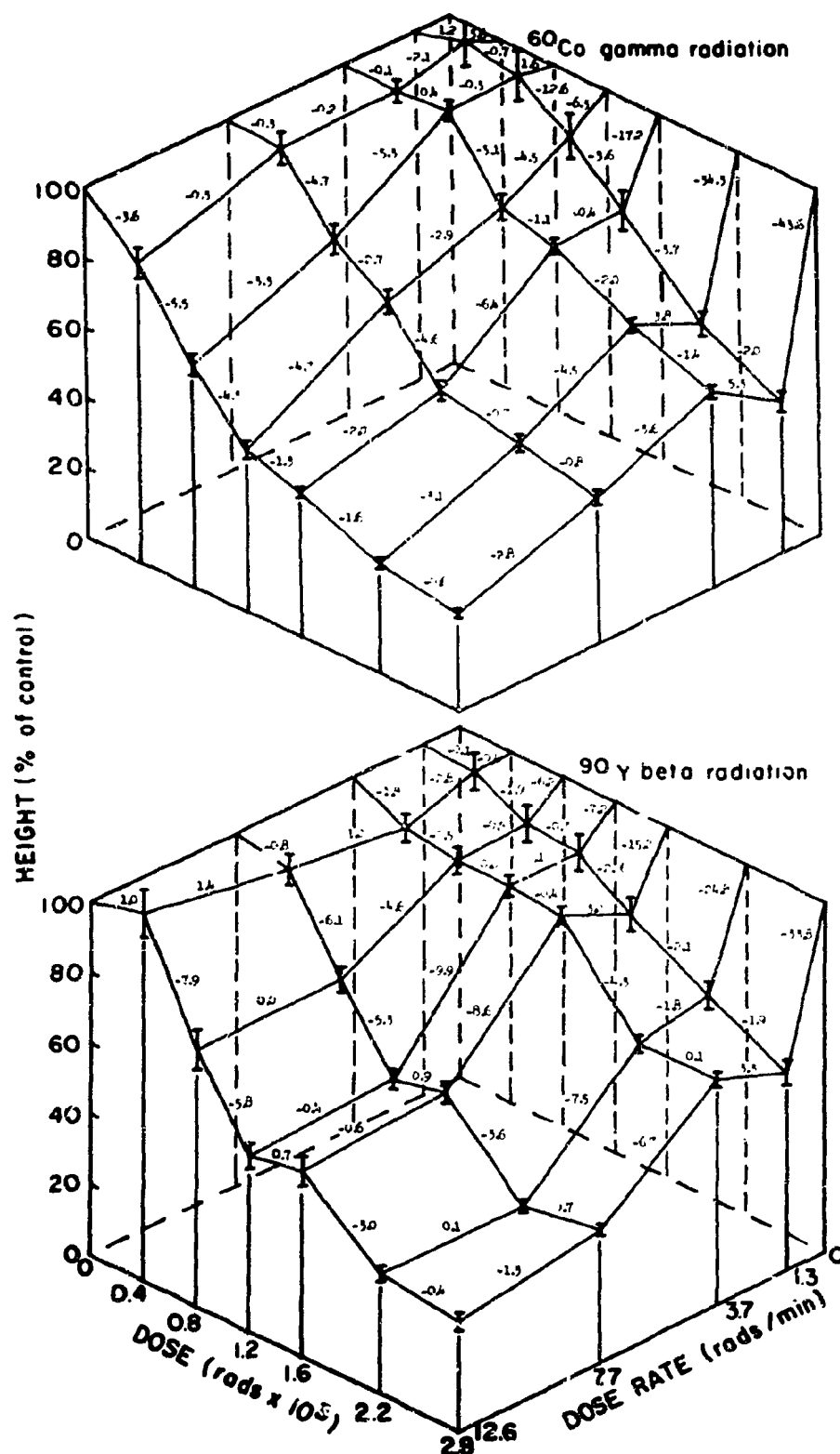


Fig. 3. Effect of gamma or beta radiation at various doses and dose rates on height of the first leaf of barley seedlings. Seeds were irradiated at 16 hr of germination. Numbers on response surface indicate changes expressed as either  $\% \times 10^{-2}/\text{rad}$  or  $\%-\text{min}/\text{rad}$ . Vertical bars indicate standard errors. Height was recorded in the steady-state phase of first-leaf growth (control  $15.2 \pm 0.5$  cm).

### Seedlings

The response surface for wheat plant survival following the irradiation of seedlings (Fig. 4) was different than that for height following the irradiation of germinating seeds (Fig. 2). At the lower doses and/or dose rates, survival was unaffected in contrast with an observed reduction in seedling height. Once within the response section, however, survival decreased more abruptly than did seedling height.

In the soybean study, plants in the unifoliolate-leaf stage were subjected to various total doses of beta and gamma radiation (separately and in combination) at various dose rates and grown to maturity under outdoor conditions. At maturity, plants were scored for height and lateral growth from the cotyledonary node (Fig. 5). Height response was dependent on total dose and independent of dose rate and type of radiation. Height was reduced to 50% of control at 2.8 krad and reached a minimum of 10% of control at a dose  $\geq 3.6$  krad. In addition to total dose, lateral growth was dependent on dose rate and type of radiation. With a total dose of 2.4 krad, the number of plants with lateral growth increased from none to 50% at 8.4 rads/min and from 44 to 100% at 17.8 rads/min as beta radiation was increased from 0 to 100% of the total dose. Essentially none of the controls and plants subjected to low doses had lateral growth, while at the higher doses all of the plants had lateral growth (branches). Lateral branch length reached a maximum at 2.4, 3.6, or 4.8 krad depending on dose rate and the amount of beta radiation in the total dose. At these total doses, length increased as the amount of beta radiation was increased; the length increase was more pronounced at the low than at the high dose rate.

The effect of gamma irradiation on soybean plant growth was influenced by the postirradiation period, as well as by dose (Fig. 6). This response surface illustrates that the growth of plants that received the higher doses changed more abruptly initially than did the growth of plants that received the lower doses. The stimulation observed at 1.0 and 1.5 krad is apparently an artifact associated with the postirradiation period. These results indicate that levels of effective dose (ED) would be influenced by the postirradiation period (Fig. 7). For any level of damage, the required dose decreased with an increased postirradiation period. In general, the change was abrupt at the earlier periods and

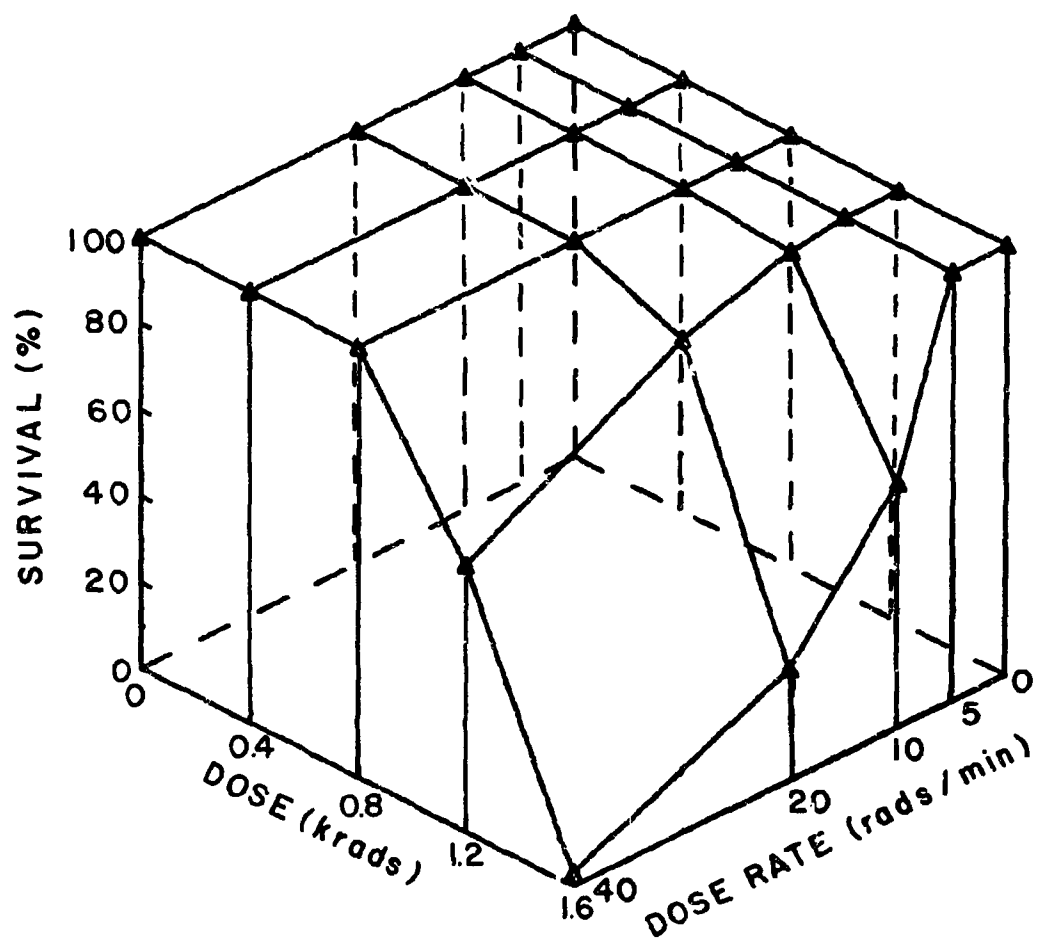


Fig. 4. Effect of gamma radiation at various doses and dose rates on wheat plants as determined by survival at maturity. Seeds were germinated in 5-cm peat pots, irradiated as seedlings, and transplanted to field plots.

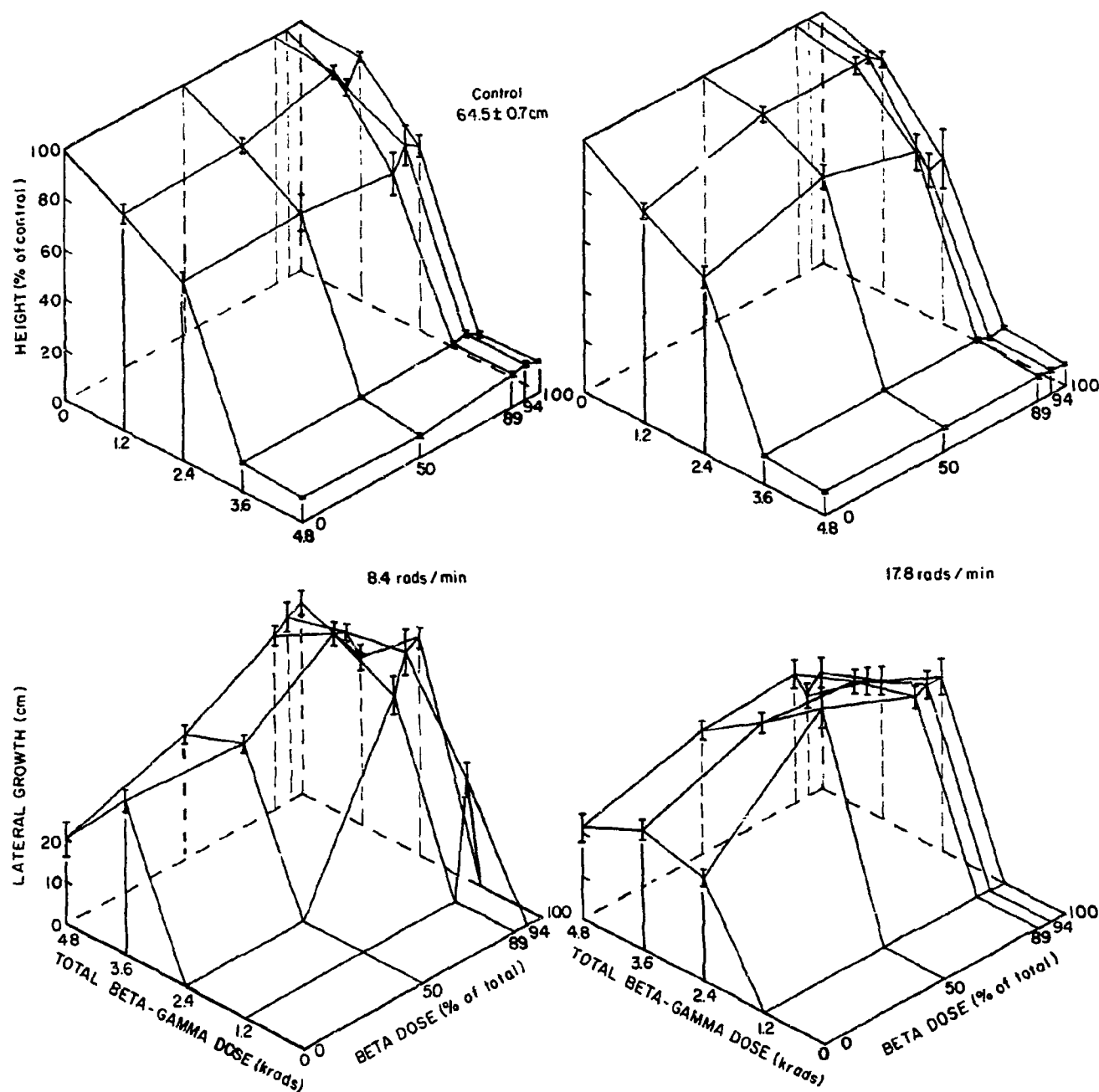


Fig. 5. Separate and combined effects of beta and gamma radiation at various doses and dose rates on height and lateral growth from cotyledonary node of soybean plants. Seeds were germinated in 5-cm peat pots, irradiated as the unifoliolate leaves unfolded, and transplanted to field plots. Indices were recorded in the steady-state phase of plant growth. Vertical bars indicate standard errors.

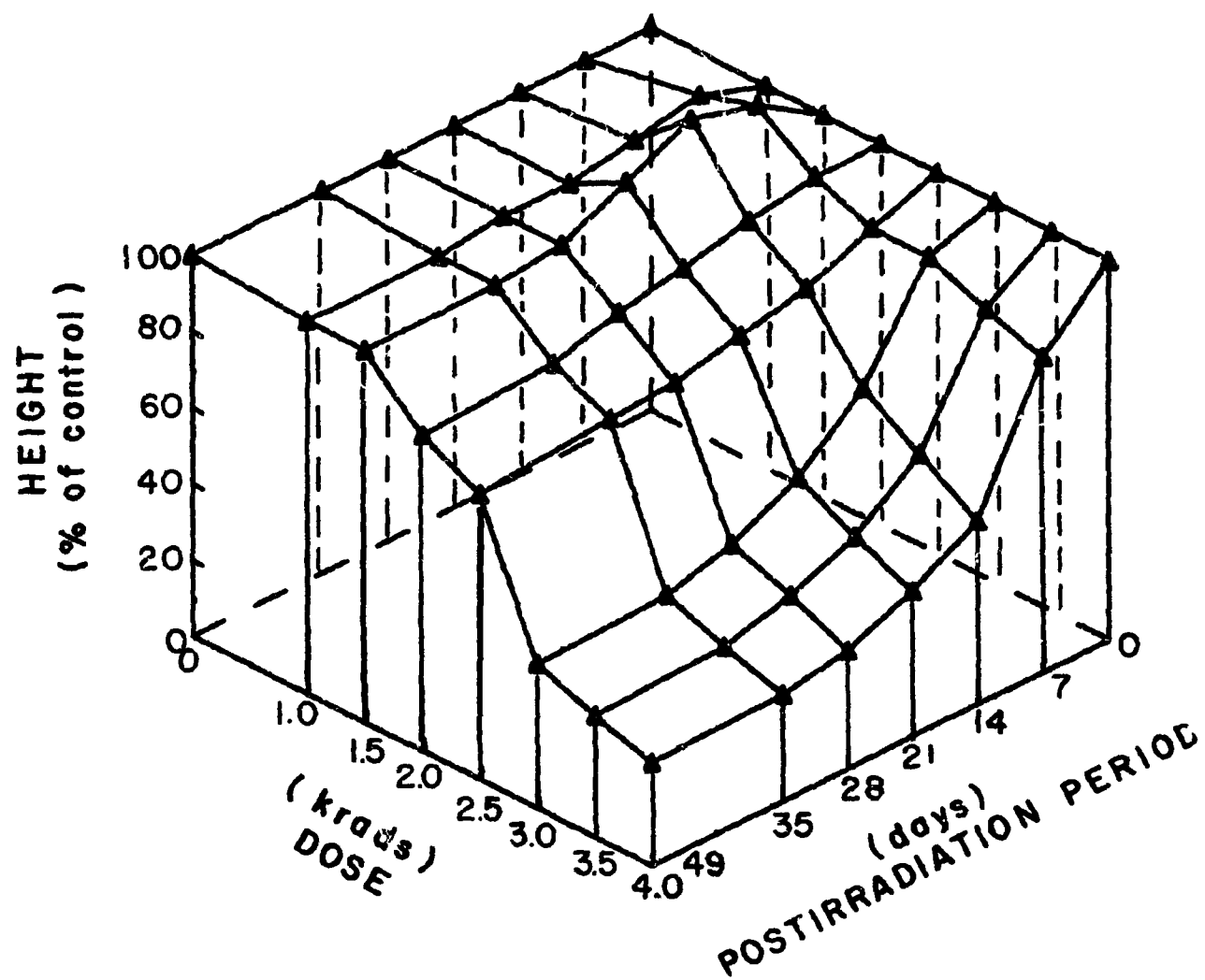


Fig. 6. Effect of gamma irradiation (50 rads/min) on the soybean plant as determined by height at various postirradiation periods. Plants were grown in large containers under outdoor conditions. Irradiation was administered at the 4-trifoliolate period in the life cycle.



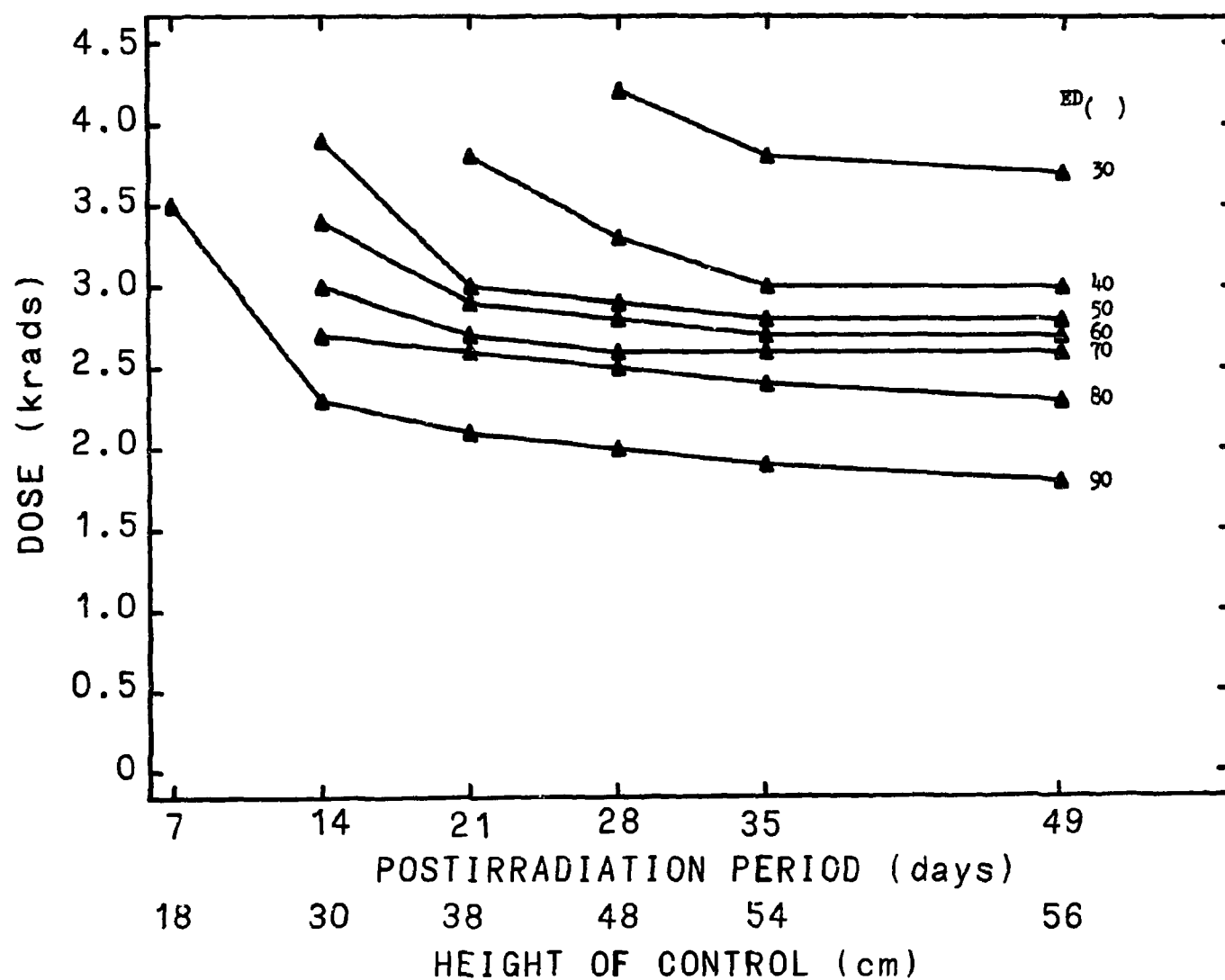


Fig. 7. Doses required to produce specific effects (ED's) on height of the soybean plant at various postirradiation periods. Values were taken from Fig. 6.

decreased as the period was increased. For example, consider the ED<sub>50</sub>. The doses required at 14, 21, 28, 35, and 49 days postirradiation were 3.9, 3.0, 2.9, 2.8, and 2.8 krads, respectively.

#### Various Stages Throughout the Life Cycle

Studies with several plant species indicate that sensitivity to gamma irradiation follows a similar pattern during their life cycle (Fig. 8). Sensitivity of all plant species increased with the progression of their life cycle, reached a maximum during the gametophyte generation, and then decreased as they approached maturity. Results indicate also the difference in sensitivity among the various species studied. Rice was considerably more resistant than were soybean, corn, and wheat. At meiosis, rice was approximately ten times more resistant than wheat and seven times more resistant than either soybean or corn. This difference in sensitivity decreased during other more resistant stages of the life cycle.

In a study with alfalfa, seedlings were subjected to various doses of gamma radiation at either 5 or 25 rads/min and grown in small containers under outdoor conditions over a two-year period. Plants were scored for survival and herbage yield at the end of each of seven successive growth periods (Figs. 9 and 10). The highest radiation dose (16 krads) reduced herbage yield at the first harvest to either 75 or 20% of control when delivered at 5 and 25 rads/min, respectively. At subsequent harvests, herbage yield was essentially unaffected by irradiation. In contrast, survival was essentially unaffected by irradiation through the second harvest, and at subsequent harvests the higher dose rate reduced survival slightly more than did the lower dose rate. The extent of survival reduction increased as harvest was delayed from the third through the seventh growth period. The data in Figs. 9 and 10 show that herbage yield per plant remained essentially constant across radiation doses; however, after the first harvest, yield per pot decreased because of decreased survival.

In another experiment with alfalfa, plants were subjected to gamma radiation at 5 and 25 rads/min at various times in relation to harvesting (Table I). This was done to simulate fallout deposition on fields during the growing season prior to and after harvesting. Results indicate that 5 rads/min (Fig. 11) reduced herbage yield to a lesser degree than did

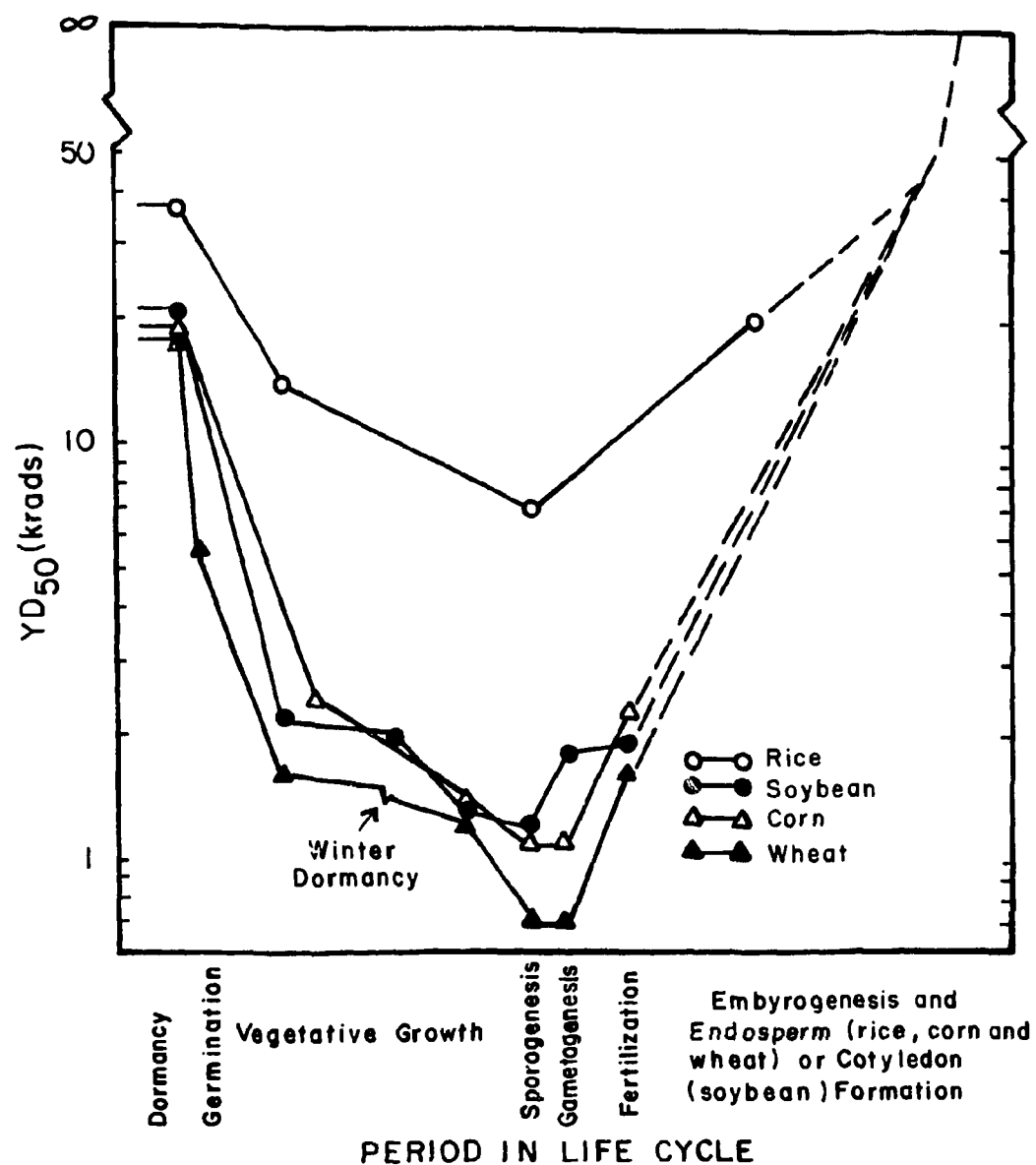


Fig. 8. Levels of acute gamma irradiation required at different developmental stages in the life cycle of different plant species to reduce seed or grain yield to 50% of control.

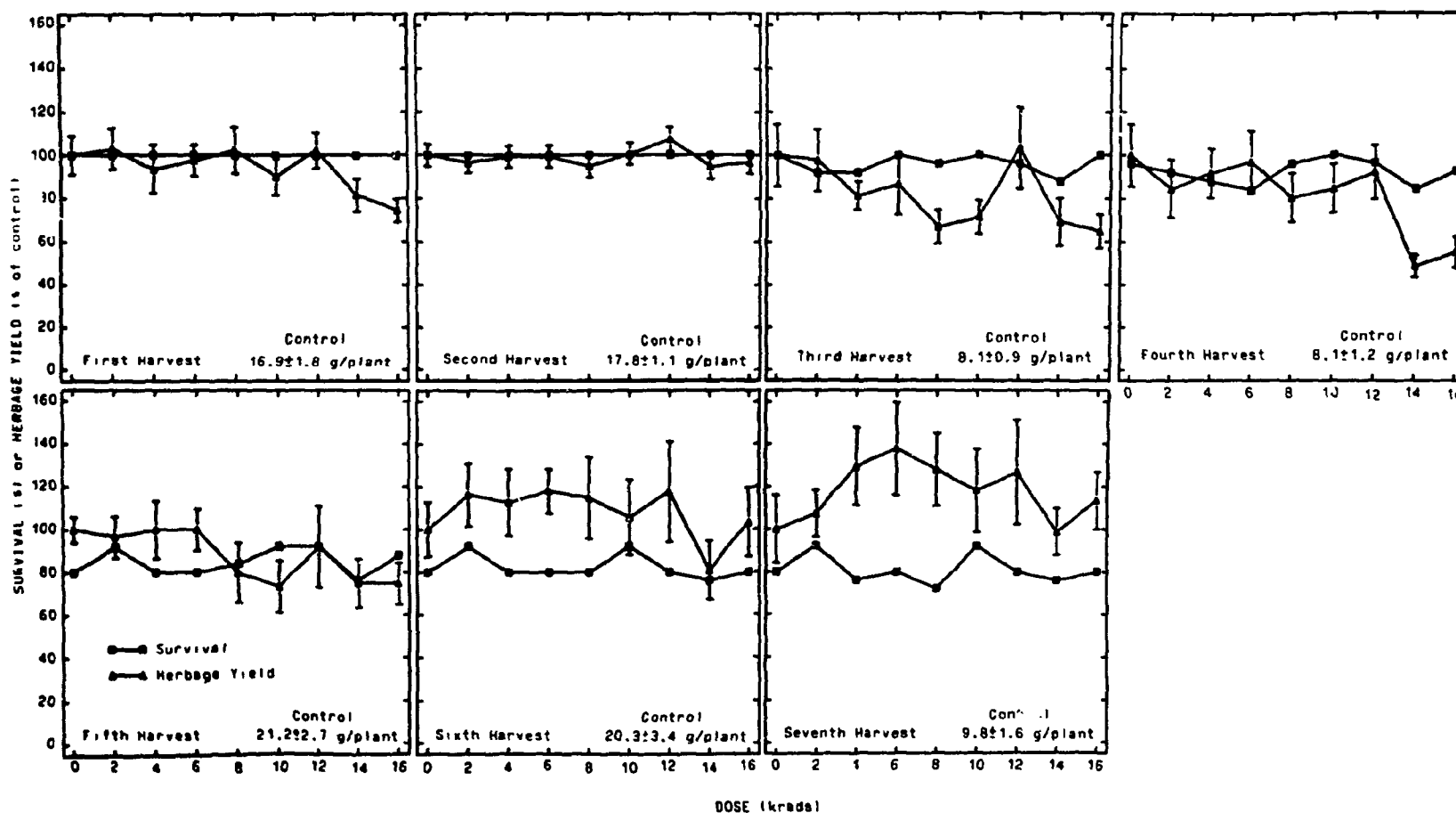


Fig. 9. Effect of gamma irradiation at 5 rads/min on alfalfa plants as determined by survival and herbage yield at successive harvests. Plants were irradiated as seedlings and grown in 12-l containers (5 plants/container) under outdoor conditions. Vertical bars indicate standard errors.

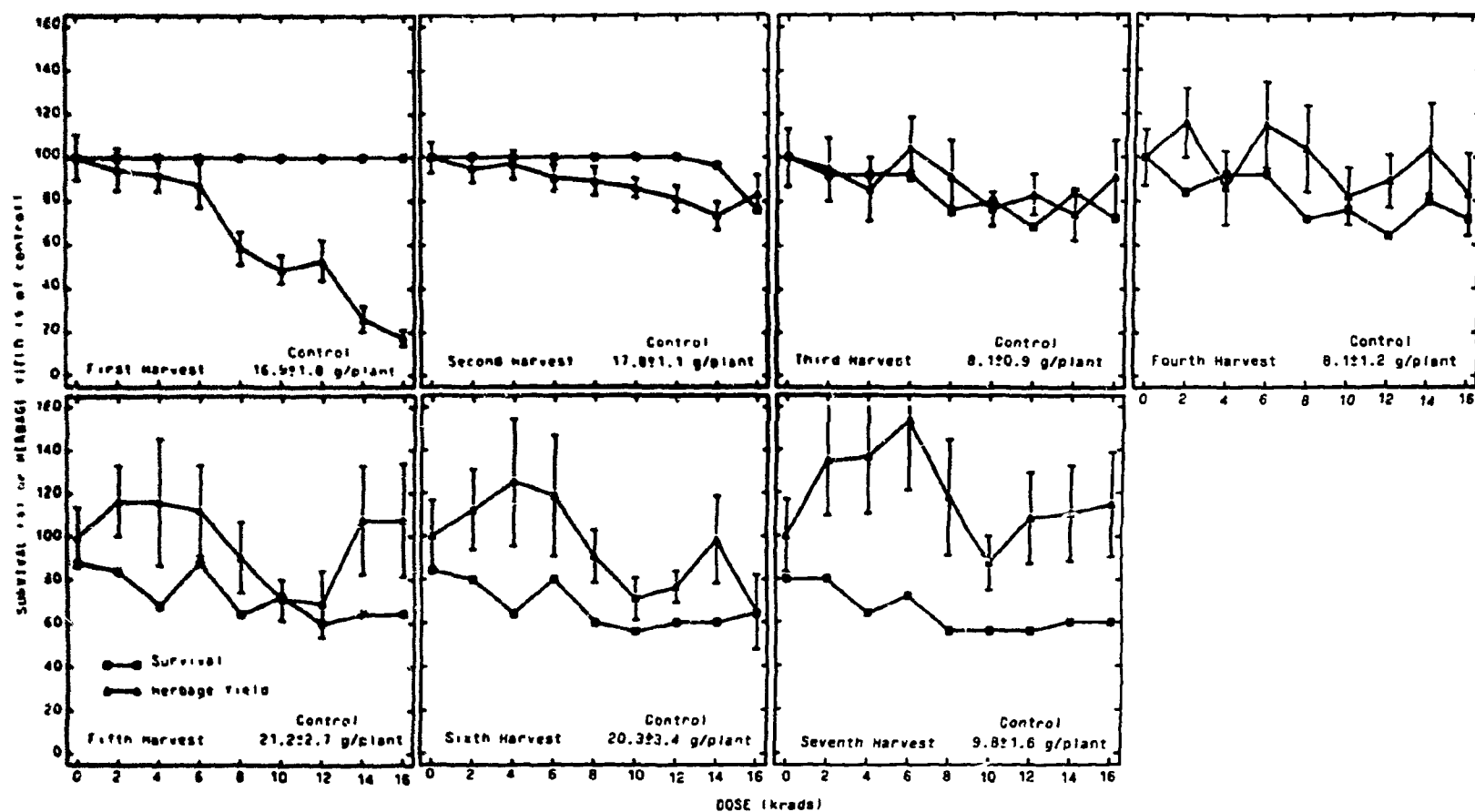


Fig. 10. Effect of gamma irradiation at 25 rads/min on alfalfa plants as determined by survival and herbage yield at successive harvests. Plants were irradiated as seedlings and grown in 12-l containers (5 plants/container) under outdoor conditions. Vertical bars indicate standard errors.

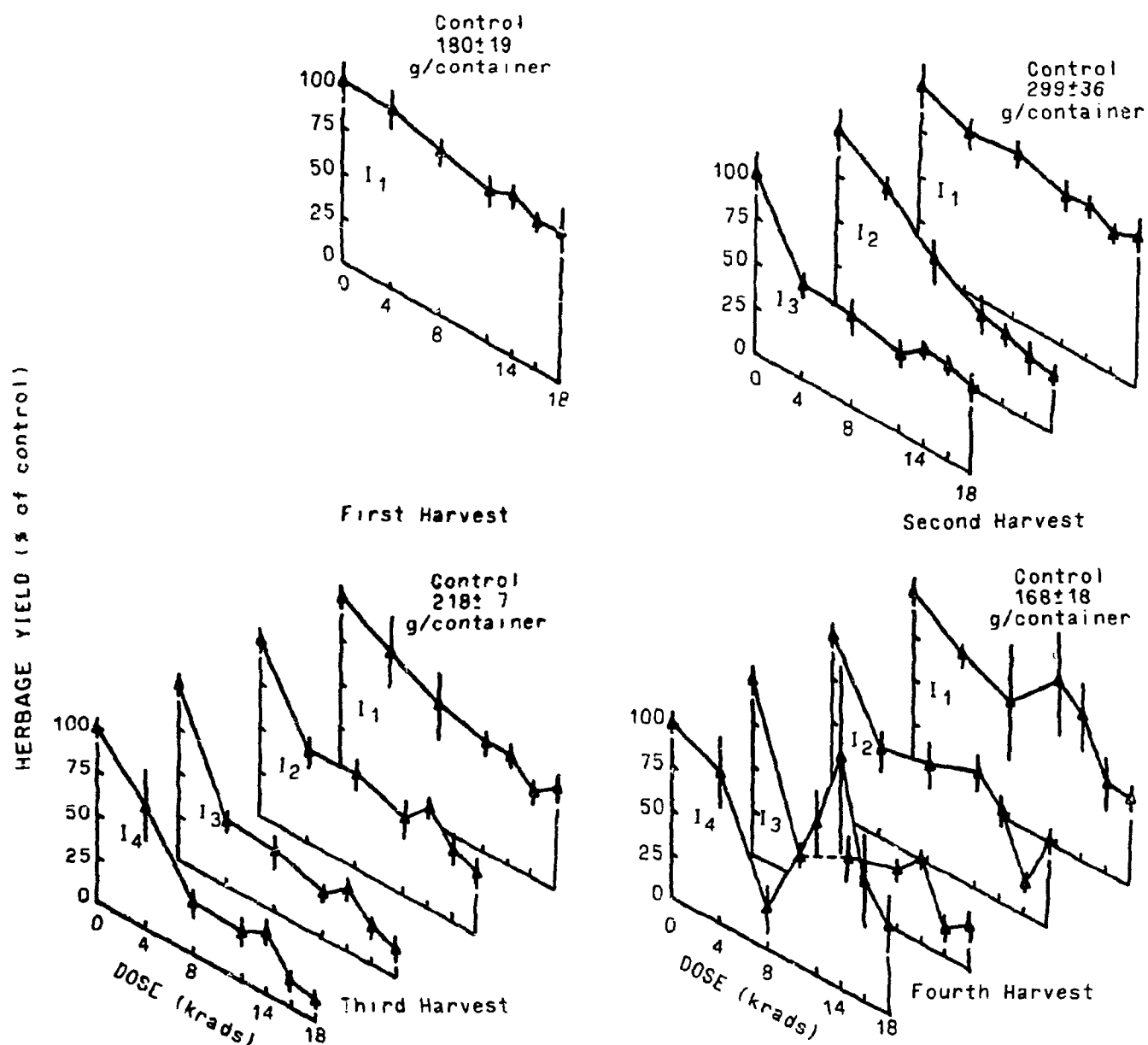


Fig. 11. Effect of gamma radiation (5 rads/min) on alfalfa plants irradiated at various periods (I<sub>1</sub>, I<sub>2</sub>, I<sub>3</sub>, and I<sub>4</sub>) between successive harvests (see Table I for irradiation and harvest schedules). Plants were grown in 100-l containers under outdoor conditions. Vertical bars indicate standard errors.

25 rads/min (Fig. 12) for each irradiation and harvest time. Herbage yield, on a per-container basis, decreased with subsequent harvests.

TABLE I  
Irradiation and Harvest Schedules for Alfalfa  
(seed sown on 4/13/73)

Irradiation	Date	Harvest	Date
First (I <sub>1</sub> )	6/20-23/73	First	7/10/73
Second (I <sub>2</sub> )	7/25-28/73	Second	8/24/73
Third (I <sub>3</sub> )	8/15-18/73	Third	9/24/73
Fourth (I <sub>4</sub> )	8/27-30/73	Fourth	6/ 5/74

Irradiation time in relation to harvesting affected herbage yield. For example, consider the second and third harvests of plants irradiated at 25 rads/min (Fig. 12). Plants irradiated 24 days (I<sub>2</sub>) were more severely affected than those irradiated 6 days (I<sub>3</sub>) prior to harvesting (second harvest). This response was reversed at the third harvest. Also, plants irradiated just prior to harvesting (I<sub>3</sub>, second harvest) responded similarly to those irradiated just after harvesting (I<sub>4</sub>, second harvest) when compared at the third and fourth harvests as an average of all doses.

At various periods of their life cycle, potato plants were irradiated at rates of either 5 or 25 rads/min and grown under outdoor conditions. Disease destroyed the plants at the period of flower-stalk elongation; consequently, they did not reach maturity. However, at this period they were scored for tuber size, number, and yield. Since the specific gravity did not change with treatment, tuber size expressed as mass per tuber is a reliable index. Specific gravity is commonly used as a measure of starch content of potatoes.

Effect of irradiation on tuber yield was greater when plants were irradiated early rather than late during their life cycle (Fig. 13). In addition, dose rate also affected tuber yield as follows: (a) at 25 rads/min, doses required to reduce tuber yield by 50% were 3.2, 3.5, 4.0, and 4.5 krad at the 3-, 6-, 8-, and 12-node stage, respectively; and (b) at 5 rads/min comparable doses were 5.0 and 6.0 krad for the 3- and 8-node stage, respectively.

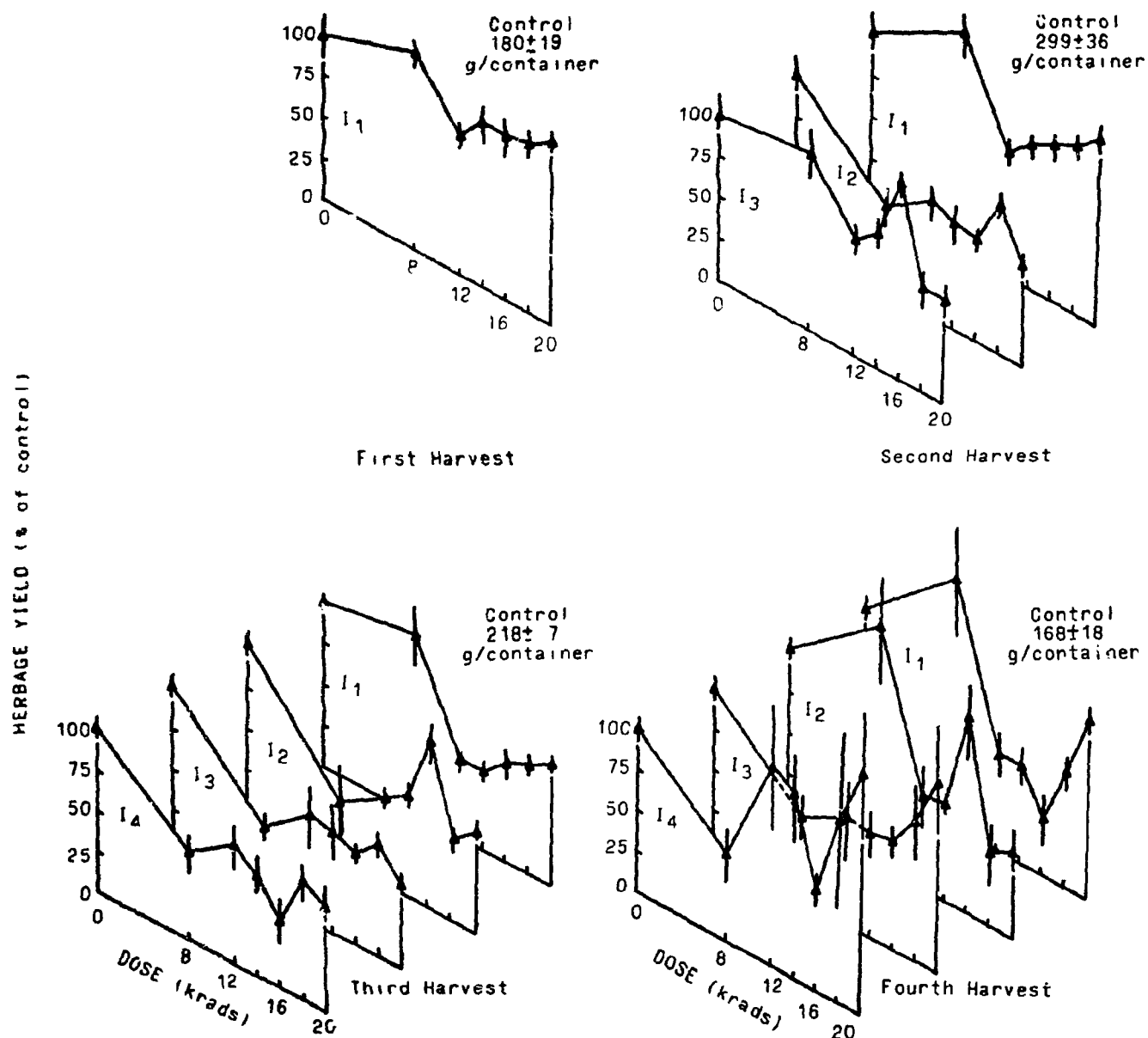


Fig. 12. Effect of gamma radiation (25 rads/min) on alfalfa plants irradiated at various periods ( $I_1$ ,  $I_2$ ,  $I_3$ , and  $I_4$ ) between successive harvests (see Table I for irradiation and harvest schedules). Plants were grown in 100-l containers under outdoor conditions. Vertical bars indicate standard errors.



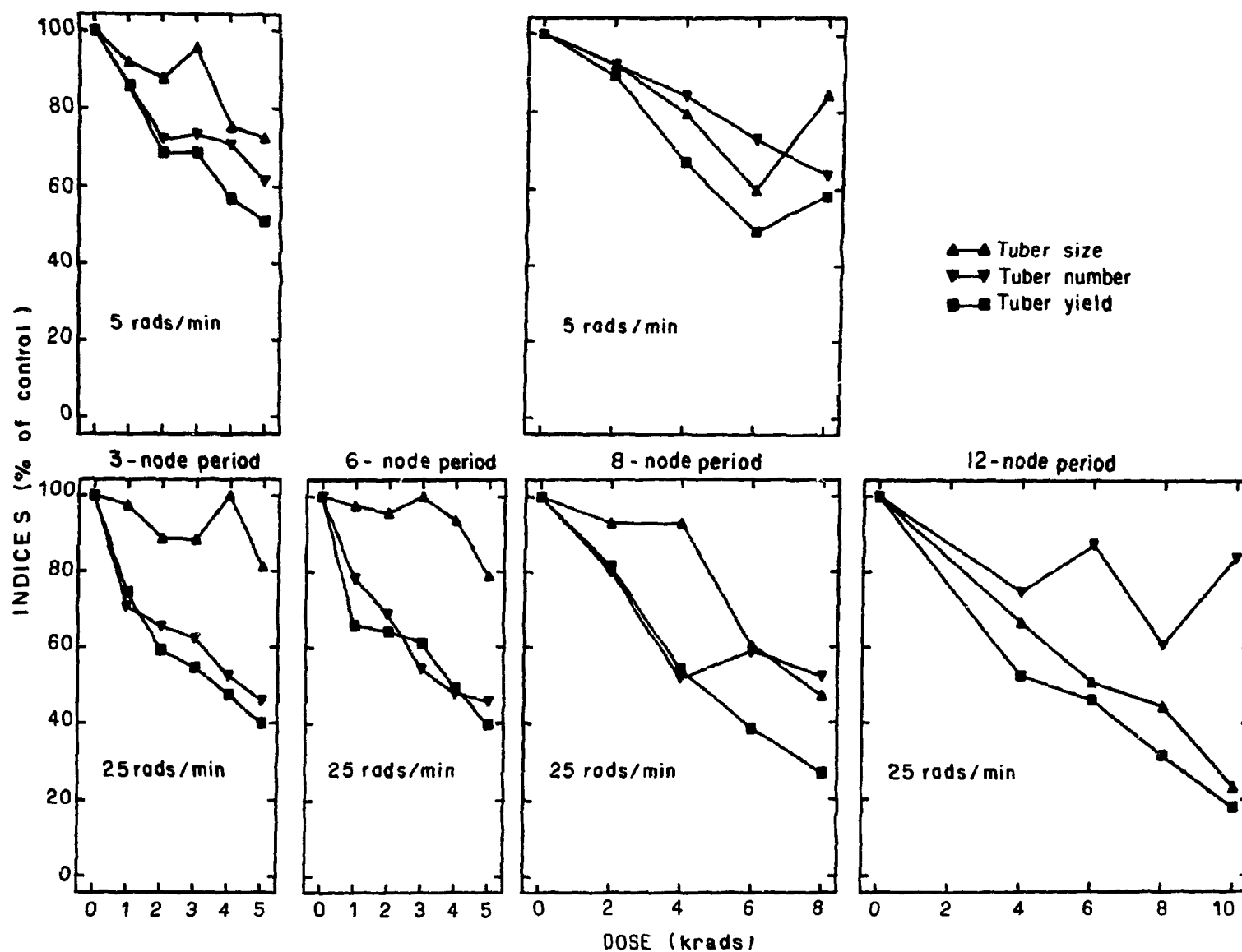


Fig. 13. Effect of various gamma radiation doses and dose rates on potato plants irradiated at various developmental stages as determined by three different indices. Plants were grown in containers under outdoor conditions (control; tuber size  $63 \pm 9$  g/tuber, tuber number  $15 \pm 3$  tubers/plant, tuber yield  $857 \pm 113$  g/plant).

Irradiation doses that reduced tuber yield also reduced the number and/or size of tubers, depending on the developmental stage at which the plant was irradiated. Correlation coefficients for tuber yield with size and number of tubers are listed in Table II. Dose rate influenced the degree of correlation as follows: (a) at 5 rads/min tuber yield was equally correlated with size and number at the 8-node stage only; (b) at the 3- and 6-node stages tuber yield was more correlated with tuber number while at the 12-node stage it was more correlated with tuber size.

TABLE II  
Correlation Coefficients of Tuber Yield to Tuber Size and  
Tuber Number (results from Fig. 13)

Developmental stage	Dose rate (rads/min)			
	5		25	
	<u>Tuber size</u>	<u>Tuber number</u>	<u>Tuber size</u>	<u>Tuber number</u>
3-node	0.89*	0.98*	0.62	0.99*
6-node			0.64	0.95*
8-node	0.90*	0.91*	0.89*	0.93*
12-node			0.98*	0.65

\*Significant linear relationship ( $P < 0.01$ ).

## DISCUSSION

In these studies, emphasis was placed on total dose, dose rate, type of radiation, plant species, developmental stage of life cycle, and postirradiation interval. Relationship of these factors can be expressed as follows:

$$r = f(d)_{dr, tr, ps, ds, pi...}$$

$$r = f(dr)_{d, tr, ps, ds, pi...}$$

$$r = f(tr)_{d, dr, ps, ds, pi...}$$

$$r = f(ps)_{d, dr, tr, ds, pi...}$$

$$r = f(ds)_{d, dr, tr, ps, pi...}$$

$$r = f(pi)_{d, dr, tr, ps, ds...}$$

where  $r$  is any response index such as survival, growth inhibition or stimulation, or seed or grain yield,  $f$  means "is a function of,"  $d$  is dose,  $dr$  is the dose rate,  $tr$  is type of radiation,  $ps$  is plant species,  $ds$  is developmental stage of life cycle irradiated,  $pi$  is postirradiation interval, and ... is other factors. The first equation states that  $r$  is affected only by variation in the dose factor; the second equation, only by variation in dose rate, etc. To be of use, the indeterminate function,  $f$ , must be replaced with some specific quantitative relationship. However, once these relationships have been developed, they would enable prediction of irradiation damage to plants under known conditions. Although definite relationships cannot be developed for each of the above factors, the extent to which each major factor contributes to plant radiosensitivity will be discussed.

### Dose

Survival curves of unicellular organisms usually show an exponential relationship with radiation dose. In contrast, survival curves for multicellular organisms show a threshold followed by an exponential decrease with radiation dose. Other modifications of this basic exponential function are commonly encountered.

For unicellular organisms the equation is

$$\frac{S}{S_0} = e^{-kD} \quad (3)$$

where  $S$  and  $S_0$  are survival of irradiated and nonirradiated populations, respectively;  $D$  is radiation dose and  $k$  is the proportionality constant.

With multicellular organisms, however, equation (3) needs to be expanded in order to account for the threshold dosage. This can be corrected for by introducing another parameter,  $n$ , into equation (3). The equation now becomes

$$\frac{S}{S_0} = 1 - (1 - e^{-kD})^n. \quad (4)$$

When graphed, and the linear portion extrapolated, the intersection with the log-survival axis is  $n$ . Other equations have been proposed, but usually equation (4) is used for most sigmoidal responses (in Okada, 1970).

In the inhibition of plant growth, one complication commonly encountered is that the response to radiation dose does not approach zero due to the initial state of the plant at the time of irradiation (Figs. 2, 3, 5, and 6). This can be corrected for by introducing another parameter,  $q$ , into equation (4). This equation now becomes

$$\frac{H}{H_0} = q + (1-q) [1 - (1 - e^{-kD})^n] \quad (5)$$

where  $H$  and  $H_0$  are heights of irradiated and control plants, respectively. When graphed, the lower linear portion is extrapolated and the intersection with log-height axis is  $q$ . Other indices, such as yield  $Y$ , are sometimes used. The results of this investigation were handled linearly because of limited data.

#### Dose Rate

With an exponential relationship, damage from irradiation at a given dose is assumed to be independent of dose rate. In the more complex models, which can be described with sigmoidal curves, damage from irradiation at certain doses is usually dependent upon dose rate.

Response curves in this investigation were sigmoidal. With wheat survival (Fig. 4), the threshold dosage was dependent upon dose rate. Threshold dosages were  $\gg 1.6$ ,  $\geq 1.2$ ,  $> 0.8$ , and  $\geq 0.8$  krads at dose rates of 5, 10, 20, and 40 rads/min, respectively. Within a given dose series, the slope ( $k$ ) and extrapolation ( $n$ ) values increased with increasing dose rates. A response such as this to irradiation is usually explained in terms of recovery (Lamerton and Courtenay, 1968). This assumes that repair proceeds concurrently with radiation damage. Hence, by decreasing the dose rate for a specific dose, less effective damage will be expressed. Results of wheat survival suggest an exponential process of recovery beyond the threshold dose rate.

When seedling height was used as an index with wheat (Fig. 2), the  $k$  and  $n$  values were reduced in comparison to those for wheat survival (Fig. 4). However, they did increase with increasing dose rate. With barley seedling height (Fig. 3), in addition to a lower  $q$  value than for wheat (Fig. 2), more height reduction occurred at a dose rate of 1.3 rads/min than at a dose rate of 3.2 rads/min. This was probably due to a change in sensitivity of the plants during the period when they were irradiated; this point will be discussed in a subsequent section.

With alfalfa (Figs. 9, 10, 11, and 12) and potatoes (Fig. 13) a dose-rate effect was evident; however, no dose-rate effect was evident with soybeans, when plant height was used as an index (Fig. 5). This was probably because the seedlings were irradiated in the lag phase of growth. This is the period during which internal changes occur that are preparatory for growth. A dose-rate effect was observed when soybean plants were irradiated in the log phase of growth (Killion, Constantin, and Siemer, 1971).

Results in this study show that a change in dose rate can cause considerable change in the  $n$ ,  $k$ , and  $q$  values. This suggests that perhaps these parameters could be used to explain dose rate. However, a separate equation would be required for each dose rate. Barley seedling results were fitted to an equation which takes dose rate into consideration (Killion, 1972). This equation is expressed as

$$\frac{H}{H_0} = a_4 + (1 - a_4) \{0.5 + 0.5 \cos [a_1 x_1 \tanh (a_2 x_2)]^{a_3}\} \quad (6)$$

where  $\frac{H}{H_0}$  = seedling height (fraction-of-control)

$x_1$  = dose (rads)

$x_2$  = dose rate (rads/min)

$a_1$  = dose parameter (rads<sup>-1</sup>)

$a_2$  = dose-rate parameter (min/rad)

$a_3$  = threshold-scaling parameter (fraction-of-control)

$a_4$  = maximum-effect parameter (fraction-of-control)

The cosine function assumes that the dose curve will, in general, have a sigmoidal shape. The hyperbolic tangent allows for the possibility that a dose-rate effect exists at a given dose above which there is no further dose-rate effect. Squared correlation coefficient for this equation with barley seedlings was 0.98.

### Type of Radiation

Under conditions of radioactive fallout, plants are susceptible to damage primarily from beta and gamma radiation. With soybeans (Fig. 5), results showed that the two types of radiation were equivalent for plant height but not for lateral growth. Length of lateral growth increased with increase in the beta-radiation component. This difference in lateral

growth at a dose rate of 8.4 rads/min was reflected in seed yield. At the 50% reduction level for seed yield, gamma radiation was approximately 1.2 times more effective than beta radiation (Killion and Constantin, 1974).

Miller and Colaiace (1971) explained lateral-growth activation on the basis of radiosensitivity differences between lateral and apical meristems. Auxin level produced by the apical meristem is also of primary importance in inhibiting lateral growth. Irradiation reduces the auxin level and hence activates lateral growth. The fact that lateral growth in soybeans increased with an increase in the beta radiation component can probably be explained on the basis of experimental procedure. However, it is not clear why 2.4 krad of gamma radiation delivered at 8.4 rads/min failed to promote lateral growth, whereas beta radiation administered under the same conditions promoted lateral growth. For the irradiation treatments, plants were placed between two beta sources to permit a minimum of tissue between the sources and the apical meristem. Consequently, the lateral meristems were shielded by the cotyledonary petioles and therefore received an attenuated beta-radiation dose. In contrast, with gamma radiation all parts of the plant received essentially the same dose.

Gamma radiation reduced height of wheat and barley seedlings (Figs. 2 and 3) more than beta radiation. This reduction was more pronounced with wheat than with barley seedlings. In a previous study with barley seedlings (Killion, 1972), equation (6) was used to compare the effects of beta and gamma radiation. Evaluation of the four parameters (namely,  $\alpha_1$ ,  $\alpha_2$ ,  $\alpha_3$ , and  $\alpha_4$ ) showed that beta and gamma radiation were equally effective in reducing height. In that study, dose and dose rate were not confounded with change in sensitivity; hence, beta and gamma radiation are assumed to be equivalent in their effect. The same dosimetry was used for wheat.

In general, the biological effectiveness of moderate-energy beta and gamma radiation is considered to be equal (Quimby and Feitelberg, 1963). This is true for height of soybean plants (Witherspoon and Corney, 1970) and barley (Conger, Killion, and Constantin, 1973).

Beta-radiation absorption can be described by an approximate exponential relationship in the initial portions of an absorption curve. However, this curve eventually turns downward toward negative infinity on a semilog plot, because a maximum range exists for a given beta-radiation spectrum (in Friedlander and Kennedy, 1962). The equation is

$$\frac{A_d}{A_o} = e^{-\lambda d} \quad (7)$$

where  $A_o$  is radiation intensity without the absorber,  $A_d$  is radiation intensity with the absorber,  $d$  is thickness of absorber, and  $\lambda$  is the absorption coefficient. In this study,  $\lambda$  was determined to be  $0.425 \text{ mm}^{-1}$  for  $^{90}\text{Y}$ . Hence, the tissue thickness required to reduce the activity to one-half of its initial activity would be

$$\ln \frac{A_d}{A_o} = \ln 0.5 = -0.425d \quad (8)$$

$$d_{1/2} = \frac{0.693}{0.425} = 1.63 \text{ mm.}$$

The range is determined from the equation (in Lapp and Andrews, 1963)

$$R = 0.542E - 0.133 \quad (9)$$

where  $R$  ( $\text{g}/\text{cm}^2$ ) is the range in Al and  $E$  (Mev) is the maximum energy of the beta radiation. Since  $E$  is 2.25 Mev for  $^{90}\text{Y}$ ,  $R$  is  $1.087 \text{ g}/\text{cm}^2$  in Al. If the tissue density is assumed to be unity, then its range is

$$\frac{1.087 \text{ g}/\text{cm}^2}{1.0 \text{ g}/\text{cm}^3} = 1.087 \text{ cm.}$$

This gives a ratio of range to half-thickness of 6.7. Also, the range in air (STP) would be

$$\frac{1.087 \text{ g}/\text{cm}^2}{1.293 \times 10^{-3} \text{ g}/\text{m}^3} = 840.4 \text{ cm or } 8.4 \text{ m.}$$

From equation (8), evidently beta-radiation dose decreases very rapidly with tissue thickness. For each increase of 1.63 mm, radiation dose would be reduced by one-half. Hence, if the beta to gamma dose ratio were 2:1 at the surface, the ratio would be reduced to 1:1 at a tissue depth of 1.63 mm. This assumes that no radioactive decay takes place. The tissue thickness would be an important factor in some crops. For example: in corn a thick, relatively nonsensitive tissue surrounds the apical meristem. Also, the apical meristem in corn and other grasses is protected by the soil during the early period of the life cycle.

### Plant Species

Sensitivity of many plant species to radiation has been determined by Sparrow and co-workers (Sparrow, Schwemmer, and Bottino, 1971). They have shown that interspecific differences in radiation sensitivity are correlated with differences in the mean interphase chromosome volume (ICV) of cells in the meristematic tissue. Interphase chromosome volume is obtained by dividing the nuclear volume ( $\mu^3$ ) by the number of chromosomes. They found that the dose required to produce a specific effect or index, such as 50% reduction in survival ( $LD_{50}$ ), multiplied by the ICV is equal to a constant; that is,

$$(LD_{50}) (ICV) = \text{constant.} \quad (10)$$

This constant would vary for a given plant species depending upon the specific index noted, as well as other factors such as dose rate and period in the life cycle irradiated (Figs. 2, 3, 4, and 8). Undoubtedly, this constant is related to the constant  $k$  in equation (3), (4), or (5).

Estimates of  $YD_{50}$  values obtained from equation (10) as well as measured values (Sparrow, Schwemmer, and Bottino, 1971) were compared with the present results for plants irradiated in the seedling period of the life cycle (Table III). Results cannot be expected to be identical because different dose rates were used. They used a 36-hr fallout-decay-simulation treatment; thus, decreasing dose rates were used. In our study, an acute dose rate was used. Except for soybean and wheat, the results are in reasonable agreement. The slight difference with wheat can perhaps be explained by variation in developmental stage (Fig. 8); however, this does not explain the difference for soybean. Results in this study for wheat and potato compare reasonably well with those of Davies (1973). Thus, ICV values apparently would provide a reasonably good index for predicting radiation sensitivity of plants. However, dose required to produce a specific effect is inversely related to the ICV. Consequently, dose change is large at small ICV's and small at large ICV's. For example, by substituting the results for  $LD_{50}$  (Sparrow, Schwemmer, and Bottino, 1971) into equation (10), the result is

$$(LD_{50}) (ICV) = 60. \quad (11)$$

By differentiation, the equation becomes



$$\frac{d (LD_{50})}{d (ICV)} = \frac{-60}{(ICV)^2}. \quad (12)$$

Hence, at ICV's of 1, 10, 20, and 30  $\mu^3$ , the changes in dose with respect to ICV are 60, 0.60, 0.15, and 0.07 krad/ $\mu^3$ , respectively.

TABLE III

Sensitivity of Crop Plants to Gamma Irradiation as Determined by  
Yield at Maturity (seedlings were irradiated)

Crop plant	YD <sub>50</sub> * (krads)	YD <sub>50</sub> <sup>†</sup> (krads)
Wheat	2 - 4	1.8
Corn	2 - 4	2.4
Soybean	8 - 12	2.2
Potato		3.2
Alfalfa	8 - 12	10
Rice	12 - 16	14

\*Based on ICV with exception of wheat and corn which were measured (Table 16 in Sparrow, Schwemmer, and Bottino, 1971).

<sup>†</sup>Based on present studies (Figs. 8, 10, and 13).

### Developmental Stage

Radiation-sensitivity changes that take place at different periods in the plant's life cycle (Fig. 8) cannot be explained completely by ICV. This is pointed out by Davies (1973) from the results of Bennett and Rees (1969). Bennett and Rees showed that the chromosome volume can change with periods in life cycle; however, the change is related to histone content rather than the DNA content.

Using seed or grain yield as an index (Fig. 8), we found in this study that all plants were most sensitive to radiation in the gametophyte generation. This is in agreement with research on barley (Hermelin, 1967), lima bean (Bottino and Sparrow, 1971), and rice (Kawai and Inoshita, 1965) but conflicts to some degree with other results for wheat and barley (Davies, 1968 and 1970). Using grain yield as the index, Davies showed that the plants were most sensitive in the early vegetative stages. As suggested by Bottino and Sparrow (1971), this difference could be caused by the plants being irradiated during anthesis rather than during meiosis.

Killion, Constantin, and Siemer (1971) showed a relationship in the soybean between radiation sensitivity and morphological development. Sensitivity to radiation was related to the kinetics of stem growth. During the log phase, sensitivity increased with extended periods of growth, reached a maximum in the middle region of the log phase, and then decreased at later periods. Plants irradiated late in the log and in more advanced phases were less affected because they had progressed more toward their completed potential growth. Seed-yield response, which was similar, lagged stem-growth response by about six days. These responses, especially stem growth, seemingly obey the law of Bergonié and Tribondeau (1906).

Cell sensitivity to irradiation varies with the phase of the cycle. If measured in terms of chromosome breakage, late prophase and metaphase appear to be the most sensitive part of the cycle (Sax and Swanson, 1941). Evidently, the germinating wheat and barley differ considerably in their kinetics (Fig. 1). Barley reached its maximum sensitivity 24 hr earlier than wheat. In wheat only a slight change in sensitivity occurred after a maximum had been reached at 44 hr. However, barley sensitivity reached a maximum at 20 hr, then decreased considerably, crossing a slight plateau at approximately 40 hr. This could account for a low dose rate being more effective than an intermediate dose rate in reducing plant height (Fig. 3). With wheat yield (Killion and Constantin, 1971b), a similar situation was encountered when plants were irradiated during gametogenesis.

To make the results now shown (Fig. 8) an analytical function, developmental stages must be expressed in terms of a quantitative factor. Since temperature is a necessary factor for plant development, it would appear to be the logical choice. However, light intensity and day length modify temperature effects, especially in photoperiodic species. This concept of plant growth has been discussed in detail by Went (1957). In corn, for example, developmental stage is related to accumulated growing degree days (for appropriate equation, see Rahn, 1971). A similar approach has been utilized for other crop plants.

#### Postirradiation Interval

Radiation effects are related to the interval between irradiation and harvest. With soybean height (Fig. 5), the ED<sub>30</sub> approached maximal effect 2.1 days later than the ED<sub>90</sub>. Internally, the effect of postirradiation interval was related to the developmental stage at which the plants were

irradiated. When one considers the progenies of irradiated plants, this is a most important factor (Killion and Constantin, 1973; Davies and Mackay, 1973). Irradiation had little, if any, effect on progenies from plants irradiated prior to anthesis; after that period, however, the progenies and the subsequent crop were severely affected by irradiation. Results with tomato have shown that fruit production is delayed by irradiation (Sparrow, Floyd, and Bottino, 1970).

The postirradiation-interval response differs for different plant species. This is particularly evident in the response of annual and perennial plants to irradiation. With annuals, the irradiation effect is observed within a season; however, with perennials, the response is varied. Irradiated alfalfa seedlings (Figs. 9 and 10) responded only at the first harvest. The three subsequent harvests within that season were essentially unaffected by irradiation. When plants were irradiated just prior to the first harvest, a response was evident at the second harvest but not at the third and fourth harvests (Figs. 11 and 12).

#### SUMMARY AND CONCLUSIONS

Results presented herein show that plant responses (survival, growth inhibition or stimulation, and seed or grain yield) to irradiation depend upon dose, dose rate, plant species, type of radiation, developmental stage irradiated, and postirradiation interval. Hence, a delineation of the plant's response to irradiation must include several factors and also consider possible interactions.

When only dose and plant species were allowed to vary, the order of sensitivity of plants to irradiation was barley  $\geq$  wheat  $>$  soybean  $\geq$  corn  $>$  potato  $>$  alfalfa  $>$  rice. Using YD<sub>50</sub> as an index to evaluate the relative sensitivity of developmental stages indicated that the change was not additive. Wheat was two, eight, and ten times more sensitive than was rice at the dormant seed, seedling, and the meiotic periods, respectively. In terms of seed or grain yield, plants were most sensitive to irradiation during meiosis. Although sensitivity of plant species to irradiation has been shown to be related to interphase chromosome volume, apparently morphological development influences this relationship.

With dose and dose rate, an interaction was evident at certain developmental stages. This was most evident in the log phase of growth.

Irradiation was more damaging delivered at high than at low dose rates when the sensitivity of the plant was relatively constant. When the sensitivity changes drastically, extremely low dose rates can be more damaging than intermediate dose rates; i.e., developmental stage confounds dose and dose rate.

Beta-radiation dose can vary markedly within a plant. This is because even a millimeter of tissue can substantially attenuate beta radiation. With gamma radiation, all parts of most agronomic crop plants would receive essentially the same dose. This was demonstrated with soybean plants in which lateral meristems received an attenuated beta dose in comparison to the shoot apical meristem. However, when dosimetry is corrected for tissue attenuation, beta radiation appears to be equivalent to gamma radiation for a specific index of damage.

Also important is the postirradiation interval at which the plant is scored for a specific index of damage. With soybean height, as well as other characteristics of annual plants, the plant would have to be grown to maturity to obtain a maximal estimation of damage. With perennials, the damage may not manifest itself for years. In the case of alfalfa, damage was evident only at the first harvest after irradiation; whereas at subsequent harvests, it appeared to recover from irradiation damage.

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We gratefully acknowledge Gary E. Spalding for the mathematical model used in the analysis of some of the data, and David S. Walker for technical assistance in conducting the experiments.

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